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Turbulence avoidance: An alternate explanation of turbulence-enhanced ingestion rates in the field

Abstract—Field observations supporting the hypothesis that wind-driven mixed-layer turbulence enhances the prey ingestion by larval fish tend not to have the resolving power to distinguish an alternative hypothesis: that the fish larvae and their prey avoid the turbulence by swimming or sinking downward to the calmer waters, thereby enhancing their concentrations and increasing encounter rates of predator and prey. Here, evidence is supplied supporting the notion of the turbulence-avoidance hypothesis, and some rough calculations are made to estimate the conditions under which it might apply, how large its effect might be, and the types of organisms that might benefit from it. It is suggested that the turbulence-avoidance behavior could lead to significant increases in predator and prey concentrations below the mixed layer only hours after the onset of wind-driven mixing. Larger larval and juvenile fish are expected to benefit the most from such a behavior because they are stronger swimmers and eat larger prey, which might also exhibit the turbulence-avoidance behavior.

In the wake of Rothschild and Osborn's (1988) paper outlining how turbulence might enhance predator-prey contact rates in the ocean, numerous models have been developed exploring the effects of turbulence on encounter and ingestion rates of larval fish or copepods (MacKenzie and Leggett 1991; MacKenzie et al. 1994; Kiørboe and Saiz 1995). The encounter rate per predator, e , is a function of the prey concentration, C , and factors affecting the relative motion between the predator and prey, β (the 'behavioral kernel' with units similar to a clearance rate of $\text{cm}^3 \text{s}^{-1}$).

$$e = \beta C \quad (1)$$

Most models concentrate on refining β because it contains the information about the immediate effects of turbulent motions. Here, I suggest that attention must also be paid to the effects of turbulence on the prey concentration C , which may

undergo significant changes due to turbulence-induced behaviors in the field. It is important to test whether these latter effects outweigh the influence of turbulence-enhanced contact rates.

Testing the influence of turbulence on encounter, ingestion, and growth rates of fish larvae in the field has led to equivocal results (reviewed in MacKenzie 2000). Although several studies have found a positive effect (Sundby and Fossum 1990; Sundby et al. 1994; Dower et al. 1998), other investigations have found no or even negative effects. Laboratory experiments using fish larvae preying on copepods (MacKenzie and Kiørboe 1995; 2000) or copepods preying on diatoms or ciliates (Saiz and Kiørboe 1995) have shown enhancement of encounter rates at moderate levels of turbulence and depressed ingestion at higher levels of turbulence, although pursuit success of fish larvae was significantly depressed by all levels of turbulence. Extrapolating such results to the field, however, is problematic: the laboratory conditions do not allow the organisms a refuge from the turbulent motions and thus restrict their natural range of behaviors.

An alternative explanation for the enhanced ingestion and growth rates of copepods and larval fish in turbulent mixed layers is that the organisms actively avoid the turbulent waters by swimming downward. Such a behavior could lead to increased plankton concentrations below the mixing layer if the organisms swim into a thinner layer than they previously occupied. Such behaviorally enhanced concentrations could lead to increased encounter and ingestion rates of predators in the submixed layer region compared to the surface-mixed layer prior to the increase in mixing. If the refuge region below the mixed layer is relatively thin—say, 5 m or less—most conventional sampling schemes would not be able to distinguish it from the mixed layer, leading to the interpre-

tation that turbulence directly affected ingestion and growth rates, rather than being a stimulus for an avoidance behavior.

There is considerable evidence that many plankters avoid actively mixing surface layers by swimming downward to the pycnocline. Mackas et al. (1993) showed that the copepods *Neocalanus cristatus* and *Eucalanus bungii* tended to be found in the pycnocline and deeper in the water column during strong wind mixing at the surface. Lagadeuc et al. (1997) found adults of the copepods *Temora longicornis* and *Pseudocalanus* sp. to avoid the surface wind-mixed layer by swimming downward. *Pseudocalanus* sp. in particular showed subsurface concentrations during the wind event two to five times higher than the surface concentrations prior to the wind event. Incze et al. (in press) showed the copepodites of *Temora* spp., *Pseudocalanus* spp., *Oithona* spp., and *Calanus finmarchicus* to move deeper in the water column during wind-induced mixing. The nauplii of all species except *Temora* also moved deeper in the water column. The rates of dissipation of turbulent kinetic energy (ε) at the depth they migrated to were approximately those of the surface layer prior to the wind event ($\varepsilon \sim 10^{-8} \text{ m}^2 \text{ s}^{-3}$). Heath et al. (1988) showed herring larvae (*Clupea harengus*) to move deeper in the water column during strong winds and that estimated mixed-layer turbulence was a strong determinant of larval vertical distribution. Lough and Mountain (1996) found a similar behavior in larval cod (*Gadus morhua*), and both Lough and Mountain (1996) and Gallego and Heath (1999) found the same behavior in larval haddock (*Melanogrammus aeglefinus*). Olla and Davis (1990) also found a turbulence avoidance behavior in laboratory experiments with larvae of the walleye pollock (*Theragra chalcogramma*).

Given the prevalence of such turbulence-avoiding behavior in both larval fish and their potential copepod prey, it is worthwhile making some rough calculations to estimate the potential timescales and implications of such a behavior. First, I calculated the rate at which plankton can exit an actively mixing surface layer of thickness z_{ml} . Next, I calculated the potential change in concentration as downward-swimming organisms randomly aggregate in a subsurface layer of thickness z_{th} . Finally, I calculated the relative change in encounter frequency driven by such a change in concentration and compared this rate to the encounter frequency driven by turbulent mixing. Throughout this paper I use the term "mixed layer" to refer to the actively mixing region and "thermocline" to denote the region in which mixing is suppressed. For deep thermoclines, the exponential decrease in ε with depth may afford a suitable refuge from turbulence within the mixed layer above the thermocline. In some cases the thermocline can be highly sheared, causing intermittent bursts of turbulence, leaving the calm region below the thermocline. In either case, I assume the organisms to migrate to a sufficiently calm region that they cease moving downward to avoid surface-generated turbulence.

To calculate the time it might take an organism swimming downward with speed w_s to exit a mixed layer of thickness z_{ml} and vertical eddy diffusivity κ , I use a solution to the reverse Fokker-Planck equation (Lande and Wood 1987).

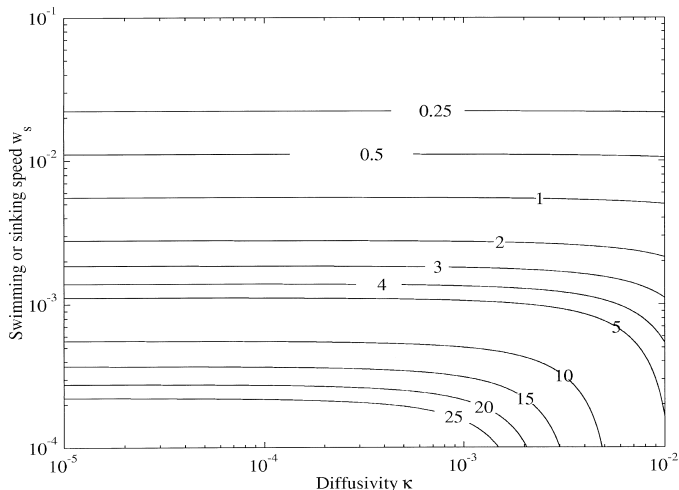


Fig. 1. Time taken (h) for a plankter swimming or sinking with downward speed w_s (m s^{-1}) to exit a 20-m-thick surface layer mixing with diffusivity κ ($\text{m}^2 \text{ s}^{-1}$). Times based on Eq. 2.

$$T_{z_{\text{ml}}}(z_0) = \frac{z_{\text{ml}} - z_0}{w_s} - \frac{\kappa}{w_s^2} (e^{-(z_0 w_s / \kappa)} - e^{-(z_{\text{ml}} w_s / \kappa)}). \quad (2)$$

Here, $T_{z_{\text{ml}}}(z_0)$ is the time taken for a swimming particle starting at depth z_0 to exit below the bottom of the mixed layer z_{ml} (Fig. 1). Organisms at the surface ($z_0 = 0$) take the longest, with deeper organisms taking progressively less time; thus, the time taken for an organism starting at the surface is a conservative estimate of the transit time through the mixed layer. The lack of slope of the contours of Fig. 1 indicates that turbulence has very little effect on the transit time of organisms with swimming speeds $>1 \text{ mm s}^{-1}$ for most reasonable levels of mixing. A plankter starting at the surface with a swimming speed of $.01 \text{ m s}^{-1}$ would exit the bottom of a 20-m thick mixed layer with diffusivity $<10^{-2} \text{ m}^2 \text{ s}^{-1}$ in $\sim 0.5 \text{ h}$. A plankter swimming at 0.001 m s^{-1} would take $\sim 5.5 \text{ h}$ to travel the same distance, except at very high turbulence levels, in which the trip would be shortened by an hour or so due to turbulent transport. Calculations using a Lagrangian model with a more realistic vertical distribution of turbulence (Franks and Marra 1994) gave essentially the same results. These transit times agree well with changes in concentration of plankton avoiding wind-mixed layers (references cited above). Copepod nauplii tend to show a weaker response to turbulence than the adults (Lagadeuc et al. 1997; Incze et al. in press). This is consistent with their swimming abilities: nauplii tend to swim at $0.005\text{--}0.002 \text{ m s}^{-1}$, whereas adult copepods swim between 0.001 and 0.02 m s^{-1} , depending on species and conditions (Mauchline 1998). This lack of response may also reflect the inability of nauplii to sense the same fluid deformations that lead the adults to react (Kjørboe et al. 1999). Small larval herring and cod swimming speeds are $0.002\text{--}0.01 \text{ m s}^{-1}$, with the lower values being the average speed and the higher values the attack speeds (MacKenzie and Kjørboe 1995). Swimming speed increases with larval size; thus, older fish larvae are able to exit a surface mixing layer faster than young larvae.

The increase in concentration below the mixed layer will depend on the initial concentration of organisms in the sur-

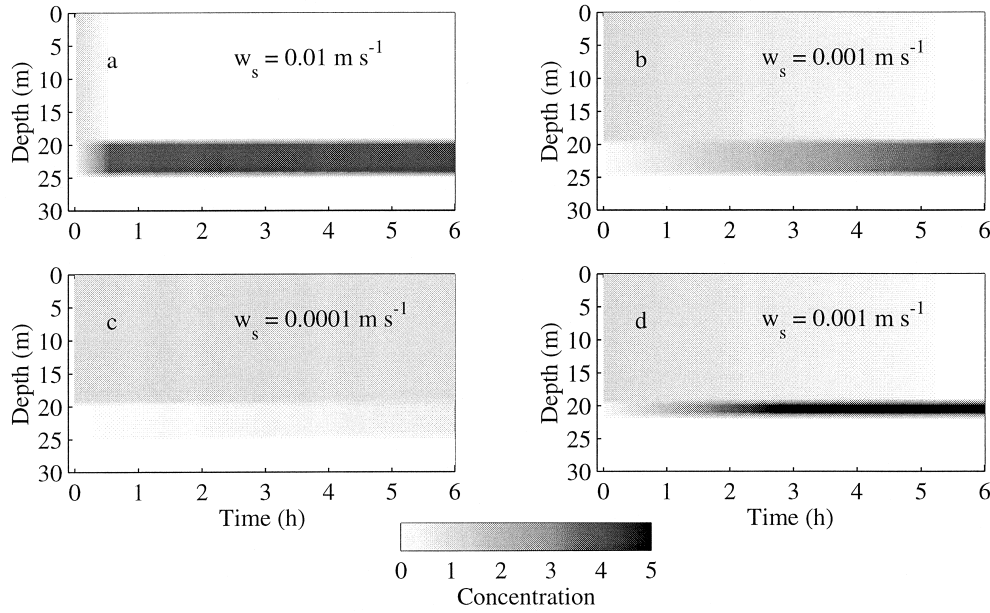


Fig. 2. Four examples of plankton swimming or sinking downward from a mixed layer (z_{ml}) 20 m thick into a calm subsurface layer (z_{th}) 5 m thick (a, b, and c) or 2 m thick (d). The initial concentration in the mixed layer was 1 (arbitrary units) and 0 elsewhere. The swimming speed is indicated in each panel. The diffusivity κ in the mixed layer was $10^{-3} \text{ m}^2 \text{ s}^{-1}$ and zero below. The final concentration would be z_{ml}/z_{th} , although this is not reached in the 6 h shown for the slower swimming speeds. Note the high concentrations in the subsurface layer for fast-swimming plankton (a) and for those plankton aggregating in a relatively thin layer (d). Times are based on Eq. 2 (see Fig. 1).

face-mixed layer $C_{ml}(0)$, the thickness of that layer z_{ml} , and the thickness of the pycnocline or thermocline region the organisms swim into, z_{th} . For the simple case of organisms of concentration C_{ml} , homogeneously distributed throughout the mixed layer, all swimming into a region of thickness z_{th} in the thermocline below the mixed layer, the concentration of organisms C_{th} in the thermocline after a time $T_{z_{ml}}(0)$ is

$$C_{th}(T_{z_{ml}}(0)) = C_{th}(0) + C_{ml}(0) \frac{z_{ml}}{z_{th}}. \quad (3)$$

If there were no organisms initially present in the thermocline region (i.e., $C_{th}(0) = 0$), then after time $T_{z_{ml}}(0)$ the concentration in this region would be a factor z_{ml}/z_{th} greater than the original concentration in the mixed layer. For a 20-m mixed layer and a 5-m thermocline region, the turbulence avoidance behavior could lead to a factor of four increase in the plankton concentration (Fig. 2). Aggregation into a thinner layer, as has been seen by Holliday et al. (1998), for example, could lead to even higher concentrations of plankton (Fig. 2d).

How would these increases in prey concentration in the thermocline affect the encounter rate of predators compared to predators and prey that remained in the mixed layer? That is, would the predators benefit from the increased prey, or would they be better off remaining in the mixed layer to allow the turbulence to enhance their encounter rates with their prey? To explore this, I calculated the fraction by which the prey concentration would have to be increased in a calm water column to give the same encounter rate as the original concentration in a turbulent mixing layer. From Eq. 1, the

encounter rate per predator is linearly proportional to the prey concentration C . The behavioral kernel for a passively sinking ambush predator such as *Acartia tonsa* in calm conditions is

$$\beta_{calm} = \pi(r_r + r_p)^2 w_s \quad (4)$$

(Kjørboe and Saiz 1995).

Here, r_r is the reactive distance, r_p is the radius of the prey, and w_s is the sinking speed of the predator. In turbulent conditions with turbulent kinetic energy dissipation rate ε , the behavioral kernel is

$$\beta_{turb} = \pi(r_r + r_p)^2 w_s + 1.37\pi\varepsilon^{1/3}(r_r + r_p)^{7/3}. \quad (5)$$

For the encounter rates in calm and turbulent conditions to be equal, we require the ratio of the prey concentrations in calm and turbulent regions to be

$$\frac{C_{calm}}{C_{turb}} = \frac{\beta_{turb}}{\beta_{calm}} = 1 + 1.37\varepsilon^{1/3} \frac{(r_r + r_p)^{1/3}}{w_s}. \quad (6)$$

This ratio is plotted in Fig. 3 for a range of ε and $(r_r + r_p)^{1/3}w_s^{-1}$. For reasonable sizes, swimming speeds, and dissipation rates, the prey concentration in the calm region would have to be less than twice the concentration in the actively mixing waters to give the same encounter rate. Discussion of other feeding strategies and organisms in Kjørboe and Saiz (1995) also supports this value. This increase in concentration seems quite reasonable by the arguments put forward above.

A more appropriate model might be one exploring the encounter rates of fish larvae, such as herring or cod.

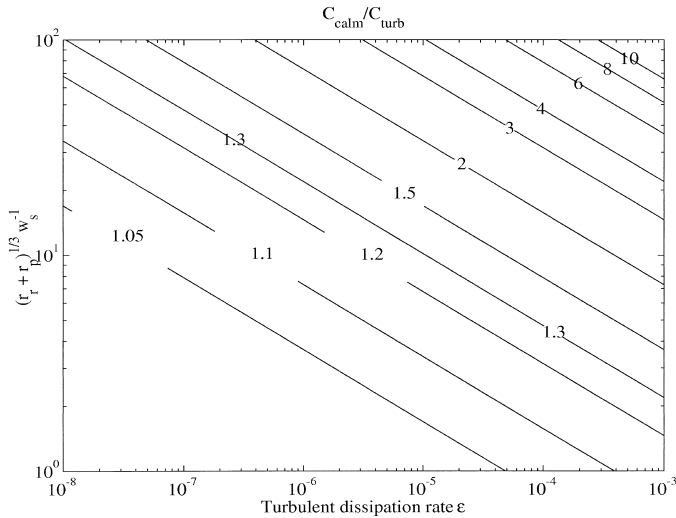


Fig. 3. Ratio of prey concentration in calm and turbulent environments for *Acartia tonsa* that gives the same encounter probability in both environments for the given dissipation rate ε ($\text{m}^2 \text{s}^{-3}$), reactive distance r_r (m), prey size r_p (m), and swimming or sinking speed w_s (m s^{-1}) (Eq. 6). For most conditions, the ratio is <2 . The ratio is >2 under very high turbulence, in which case ingestion would probably be suppressed.

MacKenzie and Kiørboe (1995) present models for pause-travel (e.g., cod [*Gadus morhua*]) and cruising (e.g., herring [*Clupea harengus*]) predators. To give similar encounter rates in calm and turbulent conditions, the model for the cruise predator gives a ratio of prey concentrations of

$$\frac{C_{\text{calm}}}{C_{\text{turb}}} = \frac{R_{\text{turb}}^2 \text{SA}_{\text{turb}} (w_s^2 + 2\omega^2)^{1/2}}{R_{\text{calm}}^2 \text{SA}_{\text{calm}} w_s} \quad (7)$$

Here, R is the reactive distance, SA the proportion of time spent swimming, and ω the turbulent velocity. I have followed MacKenzie and Kiørboe (1995) and assumed the prey velocities to be much smaller than the predator velocities and the turbulent velocities. Using values from MacKenzie and Kiørboe (1995), $C_{\text{calm}}/C_{\text{turb}}$ is ~ 1 for reasonable values of ω , indicating a very small effect of turbulence on encounter rate. Similarly, for a pause-travel predator,

$$\frac{C_{\text{calm}}}{C_{\text{turb}}} = \frac{PF_{\text{turb}}(2R_{\text{turb}}/3 + 1.41\omega PD_{\text{turb}})}{2R_{\text{calm}}PF_{\text{calm}}/3} \quad (8)$$

where PF is the pause frequency and PD the pause duration. Again, using values from MacKenzie and Kiørboe (1995), the ratio was found to be 2–3, suggesting that prey concentrations would have to be only two to three times those in moderate turbulence to achieve the same encounter rate of predator and prey.

The calculations presented above give a rough idea of the increases in prey concentration in calm waters below the surface-mixed layer that would account for any perceived increase in predator–prey encounter rates driven by turbulence. In general, such increases are small—a factor of two or less. Few field studies have been performed allowing resolution of such changes in vertical distribution; however, there are several that tend to support the hypothesis that

turbulence-avoidance behavior can lead to enhanced subsurface concentrations. As mentioned above, Lagadeuc et al. (1997) showed subsurface increases in *Pseudocalanus* sp. adults of two to five times the prewind surface concentrations, presumably because of a downward migration in response to surface mixing. Incze et al. (in press) found some of the highest copepodite concentrations recorded during their study in the 20–25-m submixed layer stratum during a wind event that raised ε to $\sim 10^{-6} \text{ m}^2 \text{ s}^{-3}$ in the upper 15 m. Lough and Mountain (1996) generally found haddock and cod larvae to have their peak abundances in the low- ε subsurface pycnocline region when the surface layer was actively mixing ($\varepsilon > 10^{-8}$ – $10^{-7} \text{ m}^2 \text{ s}^{-3}$). Thus, it seems that when wind forcing causes enhanced mixing of the surface layer, some plankton and fish larvae avoid the turbulent surface layer by swimming downward (or possibly upward in the case of bottom-generated turbulence), leading to enhanced subsurface concentrations. The increase in concentration in the calm waters may be great enough to enhance feeding success as much or more than an increase in turbulence-induced encounter rates in the mixed layer.

A significant benefit of the turbulence avoidance mechanism is that the organisms would be feeding in a calm environment. MacKenzie et al. (1994) suggested that the ingestion rate of larval fish had a dome-shaped relationship to turbulence: high levels of turbulence decreased capture success as the prey moved out of the capture region too quickly. MacKenzie and Kiørboe (2000) took the intermittency of turbulent motions into account and showed that individual pursuit success significantly decreased with increasing turbulence. Thus, the increase in encounter rates between predator and prey in a turbulent layer may not lead to increased ingestion rates. However, a turbulence-avoidance strategy could lead to enhanced prey concentrations and concomitant increases in ingestion under relatively calm conditions.

Organisms that would most benefit from the turbulence-avoidance behavior are those that can swim fast enough to exit the mixed layer on relevant timescales and that eat prey that also show this behavior. The relevant timescales are determined by the rate of increase of mixed layer turbulence after the onset of wind (hours), and the diel periodicity of surface irradiance (since most plankton and fish larvae have a light-mediated diel vertical migration, and fish larvae are visual feeders). Thus, organisms swimming faster than a few millimeters per second would be the most likely to be able to exploit this mechanism. Because copepod nauplii swim relatively slowly and most small fish larvae eat nauplii, the turbulence-avoidance mechanism may only benefit larger fish larvae and juveniles that eat larger planktonic prey. Intriguingly, Dower et al. (1998) found that fish larvae feeding under turbulent conditions tended to have fewer, but larger, prey in their stomachs. Their sampling, however, could not determine where the larvae were feeding or whether they were exploiting subsurface prey patches.

The suggestion here is that behavioral responses to turbulence can increase exposure to prey in a manner that would be invisible to experiments sampling at the wrong scales. Distinguishing the two mechanisms (turbulence-enhanced ingestion and concentration changes induced by turbulence-avoidance behavior) in the field will be difficult. It

will be necessary to demonstrate a change in concentration driven by a turbulence-avoidance behavior (as distinct from horizontal advection of horizontal gradients); it will be necessary to quantify the turbulence dissipation rates in situ; it will be necessary to have fine vertical sampling resolution of biological fields; it will be necessary to establish where predators are feeding and to quantify their ingestion rates; and it will be necessary to sample with and without turbulent mixing. Several studies have been performed which meet most of these requirements (Lough and Mountain 1996; Gallego et al. 1999; Incze et al. in press), but it will take considerably more work to determine the conditions and organisms that might benefit from a turbulence-avoidance behavior. Experiments in regions of bottom-enhanced turbulence (e.g., around tidal fronts) might give useful insights because the organisms would then have to migrate upward to avoid the turbulence or find a calm region above the bottom boundary layer, but below the surface-mixed layer.

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